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REPETITIVE CYCLES OF BIOLUMINESCENCE AND SPAWNING IN THE POLYCHAETE, *ODONTOSYLLIS PHOSPHOREA*

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Abstract

Spawning by large numbers of the marine polychaete, *Odontosyllis phosphorea*, occurred at fortnightly intervals. The animals appeared at the surface of the water shortly after sunset and luminesced and spawned for approximately 30 minutes. The spawning was correlated with the monthly lunar and tidal cycles and lasted from June through October.

Introduction

Polychaetes of the genus *Odontosyllis* from Bermuda show spawning swarms throughout the year, with lunar periodicity: shortly after sunset, the bioluminescent worms appear at the surface, where they pair and mate, for several days immediately after full moon (Galloway and Welch, 1911; Huntsman, 1948; Markert *et al.*, 1961). Similar behavior has been reported for two other species of this genus: one from Puerto Rico (Erdman, 1965) and another, *Odontosyllis phosphorea,* from British Columbia (Potts, 1913); lunar periodicity in the latter species, however, has been questioned by others (Fraser, 1915; Berkeley, 1935). Still other species of this genus spawn only once a year (Haneda, 1971; Daly, 1975; Horii, 1982). We have observed spawning swarms in *O. phosphorea* from southern California, which are similar to those described in the Caribbean, except that the spawning peaks are strongly seasonal and occur at fortnightly intervals: *i.e.,* follow a semi-lunar rhythm rather than a lunar rhythm, as reported for other species of this genus.

Materials and Methods

Observations were carried out from a 3 × 24 m floating dock in De Anza Cove, Mission Bay, San Diego. The dock is oriented north-south, with the east side facing the shore. Observations were made on the shore-side, which comprised a maximum area of 530 m^2 of water surface. The dock is connected to shore by a raised walk. The distance from the edge of the dock to the high water mark on shore was ~32 m and to the low water mark, ~10 m. The water depth on July 12, 1982, at 19:15 (low tide = 19:49) was 2.3 m at the south end of the dock and 3.0 m at the north end. Luminescing *Odontosyllis* swimming at the surface were counted by two observers walking along the edge of the dock using hand tally counters. Each observer monitored one-half of the water surface; and one observer also kept time with a stopwatch. An individual *Odontosyllis* was recognized by the greenish luminescence produced by the swimming animal. A complete count of the area could be made in one minute, even during peak activity. Records were kept of the direction and

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strength of the wind, condition of the water surface, surface water temperature, phase and position of the moon (when visible), condition of the tide, and overhead cloud cover.

The times (PST) of sunset, civil twilight, moonrise, and moonset, and phase of the moon were calculated for San Diego (32.46°N) using standard tables (*Nautical Almanac for 1982,* U. S. Naval Observatory, 1980); plotted tides were predictions for San Diego (*Tide Table for 1982,* NOAA, 1981). The tidal difference between the Pacific Ocean entrance to Mission Bay and De Anza Cove is negligible. Normal probability curves and standard deviations were calculated from the observed data points (Alder and Roessler, 1968).

Specimens of *Odontosyllis* were collected with a 90 ml ladle or a fine mesh net. Each individual was immediately placed in a separate container. To determine the sex of the animal, the coelomic cavity and reproductive organ were dissected microscopically and the type of gamete was determined. The number of eggs, and, in some cases, the number of eggs already undergoing cleavage, were determined in water samples collected at the same time as the specimen. Counts were made within one hour after collection, using a dissecting microscope. Control water samples were also collected before and after each night of observation. Specimens were collected when swarming activity was at its peak.

Results

The first flashes of light after sunset were usually from males. They swam in a relatively straight line while the posterior section of the body luminesced internally. A bright burst of luminous secretion was produced intermittently, forming a luminescent trail. This trail hung at the surface of the water for about a minute before dispersing. Water samples collected with such worms often contained spermatozoa. The females began flashing shortly after the males. They appeared at the surface of the water swimming in tight wiggling circles. The body as well as the secretion it discharged were brightly luminescent. Sometimes a male and a female were observed swimming together in a small circle. The water collected with such females frequently contained eggs, and the body was nearly devoid of eggs when subsequently examined.

A fully elongated adult *Odontosyllis* was 20 to 30 mm in length and was about one millimeter in width. Eggs were ~ 15 μm in diameter. When maintained in filtered sea water at room temperature ($\sim 21°C$), fertilized eggs began cleavage and reached the gastrula stage after ~ 12 hours. The ciliated gastrulae actively swam in circles near the surface of the water; they developed into early trochophores after two days and into full trochophores after four days. Each was characterized by a well developed apical tuft, prototroch, growth zone, and pygidium. The trochophores had four black eye spots and the body showed signs of segmentation. The trochophore larvae did not luminesce when tested with $MgCl_2$ and KCl. However, within a month they reached 40 μm in length, developed parapodia, and possessed the ability to luminesce. During peaks of swarming in July and August, 1982, egg counts ranged from 35 to 63/ml (8 counts); sex ratio (males/females) varied from 0.3 to 0.6 (3 samples).

Counts of luminescing worms on a typical high-intensity spawning date are presented in Figure 1. The worms appeared about 17 minutes after sunset, the last was seen about 32 min later, and peak abundance was about 33 min after sunset. The data show a reasonably good fit with a calculated normal probability curve. Similar curves were derived for all observation dates on which worms were seen between July and October. The centers of these spawning peaks (mean time relative

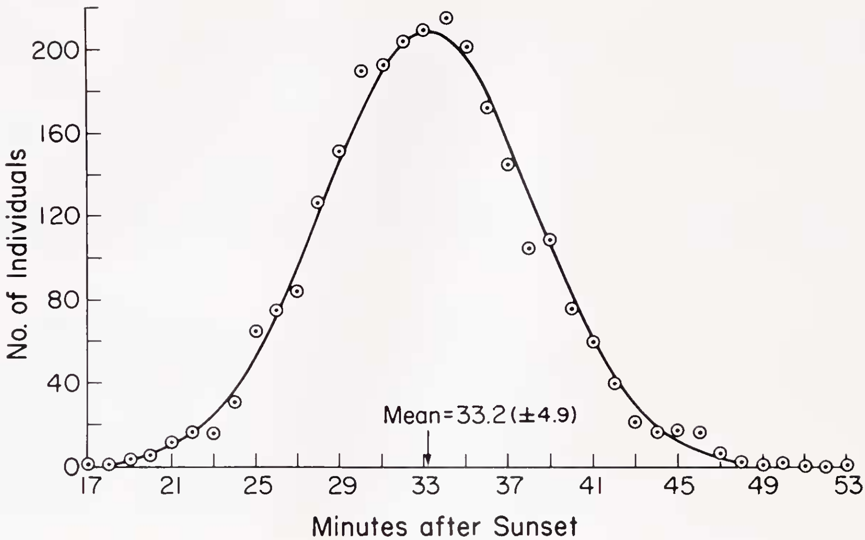

FIGURE 1. Plot of the number of *Odontosyllis* appearing after sunset on 9 August 1982. Solid line represents the normal probability curve calculated from the observed data points. Arrow indicates the mean minutes after sunset (time of peak abundance of the worms) and standard deviation.

to sunset) showed a tendency to occur progressively earlier during July, to reach a minimum in early August, and to occur progressively later thereafter, with a total seasonal range of about 30 min (Fig. 2). The days were becoming shorter (*i.e.*, sunset occurred earlier) throughout this interval. The length of twilight (~24 to 28 min), the time the full moon was in the sky (~9.5 to 11.2 hour), and weather conditions—even strong wind and overcast sky—had no apparent effect on the daily or fortnightly timing of spawning swarms.

The first sighting of *Odontosyllis* was made on 13 May (last quarter moon, 15 May) when 26 worms were counted. On 15 May, many more worms were seen, but not counted. Subsequently, worms were observed on 27 May (not counted; first quarter moon, 29 May) and on 16 June (30 counted; last quarter moon, 14 June). Thereafter, regular counts were taken. Figure 3 shows a plot of number of *Odontosyllis* observed, high and low water predictions for the tide, surface water temperature, and phases of the moon against dates of observation. The observations representing each fortnightly peak show a reasonably good fit with a calculated normal probability curve. The results show that swarming by *Odontosyllis* follows a semi-lunar cyclic pattern, with peak spawning coinciding approximately with the time of minimum variation in tidal amplitude, as well as with the first and last quarter phases of the moon. The cumulative difference between the days of peak swarming and the corresponding days of the quarter moon over the interval from late June to late October was −0.1 day; individual peaks varied from −2.9 to +2.7 days. The duration of bioluminescence and spawning ranged from 27.7 to 44.9 min between July and October, with a mean of 34.9 min. As surface water temperature rose in July, the *Odontosyllis* swarm populations increased to a maximum peak between 3–15 August. Thereafter, as the surface water temperature gradually fell, the peaks decreased in height, with the exception of a large peak between 6–12 October. No *Odontosyllis* were observed during regular searches, centered around times of first and last quarter of the moon, between 1 November and mid-April,

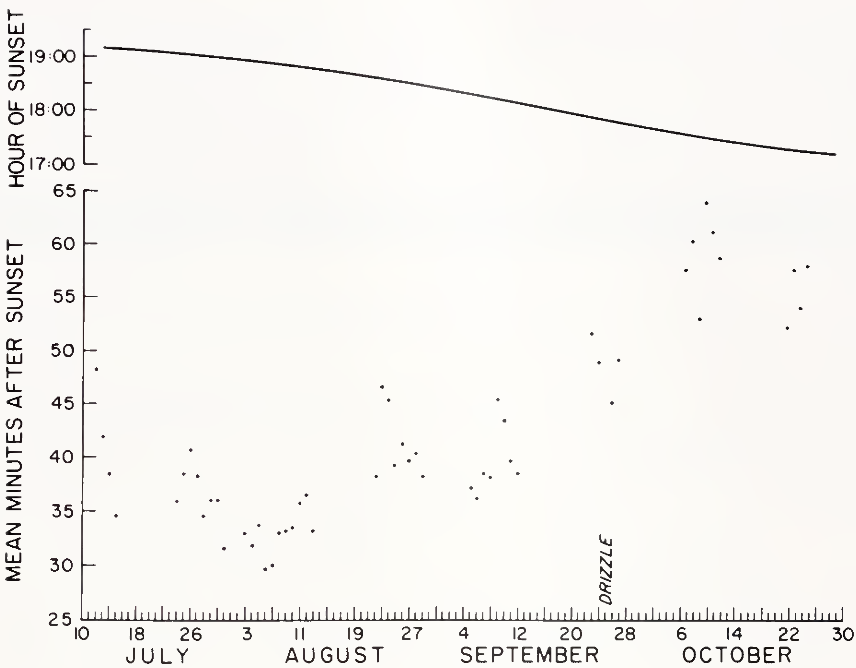

FIGURE 2. Plot of the mean minutes after sunset and time of sunset against dates of observation, July–October, 1982.

1983, as the surface water temperature reached a low of 14.0°C on 4 February. Two worms were seen on 19 April (first quarter moon) and the onset of more intensive swarming was signalled by a count of 80 worms on 3 June, by which time water temperature had risen to 22.0°C.

DISCUSSION

The data in Figures 1–3 indicate three rhythmic components in the reproductive behavior of *O. phosphorea:* a seasonal cycle, with peak spawning in the warm-water months of July to October; a fortnightly cycle, with spawning on dates corresponding roughly with first and last quarters of the moon (and hence, with neap tides); and a strong daily cycle, with spawning confined to less than an hour, beginning shortly after sunset. It is conceivable that water temperature itself influences spawning on a seasonal basis; the observations of Fraser (1915) suggest a much more seasonally restricted spawning of *O. phosphorea* in the colder waters of British Columbia. We cannot determine from the present data whether endogenous factors are involved in the fortnightly and daily rhythmicities. The semi-lunar rhythm may be directly evoked by the tidal regime, or it might represent an endogenous rhythm, perhaps synchronized by moonlight. Neumann (1976, 1978), in his laboratory studies of the reproduction of the marine midge, *Clunio marinus* (which also shows annual, semi-lunar, and daily rhythmicity), demonstrated that it is possible to induce fortnightly rhythms in the breeding by either artificial moonlight (a few days per month) or simulated tides, together with a light-dark cycle.

The fact that *O. phosphorea* shows a semi-lunar rhythm of spawning, and not a lunar rhythm, as reported for other species of this genus from the Caribbean

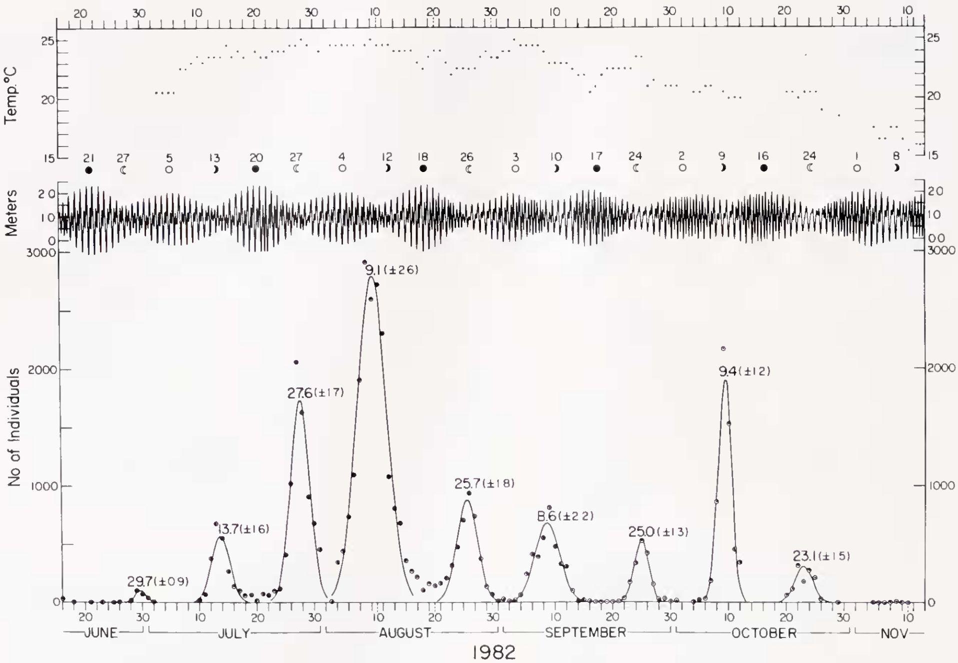

FIGURE 3. Plot of the number of *Odontosyllis* appearing, high and low water tide predictions for San Diego, surface water temperature, and phases of the moon against dates of observation, June–November, 1982. Solid line represents normal probability curves for each activity period calculated from total counts taken each evening. The values given above each peak represent the calculated mean date of peak abundance of the worms and standard deviation. The percentage of total worms (43,983), appearing in each activity period peaks, was as follows: 28 June–2 July, 0.53; 10–18 July, 5.11; 23–31 July, 16.76; 3–15 August, 40.87; 22–30 August, 9.06; 4–14 September, 8.41; 22–28 September, 3.82; 6–12 October, 12.71; and 20–26 October, 2.73.

(Markert *et al.,* 1961; Erdman, 1965) suggests that regardless of proximate factors, the behavior of the worms in Mission Bay is an adaptation to tidal conditions which recur at fortnightly intervals. In this connection, we note that during neap tides, there is minimal tidal flushing of an enclosed embayment, meaning that the progeny of spawning worms are able to complete their early larval development in near proximity to the adult habitat.

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